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Ecology of spawning humpback chub, *Gila cypha*, in the Little Colorado River near Grand Canyon, Arizona

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Synopsis

The morphologically unique and endangered humpback chub, *Gila cypha*, is found in canyon-bound reaches of the Colorado River and its tributaries. Now limited to six isolated reproducing populations, this species is believed to have been once distributed over a large portion of the mainstem river. Because the species inhabits remote canyon areas, little is known about its spawning ecology. The largest remaining population occurs in the lower Little Colorado River (LCR) near Grand Canyon, where we conducted a three-year study of spawning ecology during spring (March-June) 1993–1995. We analyzed seasonal patterns of movement, population density, relative condition, spawning scores, and frequency of ripe condition and fin abrasions and compared these data with seasonal discharge and water temperature to determine spawning phenology and ecology. Spawning commenced in late March, peaked in mid-April, and waned in mid-May. A high proportion of males remained ripe over this period, whereas ripe females were relatively abundant only in April. Increased densities of adult fish in March-April and rapid declines in May-June coupled with recaptures of 18.4% of these adults in the Colorado River suggest that a portion of the population migrated from the Colorado River into the LCR to spawn and then returned. Ripe males aggregated in areas of complex habitat structure with high angular variation in bottom profiles (matrix of large boulders, travertine masses combined with chutes, runs and eddies, 0.5–2.0 m deep) and were associated with deposits of clean gravel. Ripe females appeared to move to these male aggregations to spawn. Near-spawning (including gravid) females and non-spawning fish used similar habitats and were segregated but close (< 50 m) to habitats occupied by aggregations of ripe males. Abrasions on anal and lower caudal fins of males and females suggest that spawning involves contact with gravel substrates, where semi-adhesive eggs are deposited and fertilized. The findings of this study should aid recovery efforts for humpback chub by identifying spawning habitat within the historic distributional range where additional spawning stocks could be established.

Introduction

The remoteness and rugged character of the Grand Canyon, especially the turbulent Colorado River, hindered studies of ichthyofauna before the mid-20th century. Thus it is not surprising that the morphologically unique humpback chub, *Gila cypha,* was not described until 1945 (Miller 1946) and regular surveys of Grand Canyon fishes were not conducted until the 1960s. Since its discovery in Grand Canyon, the humpback chub has been found in other remote canyon reaches of the upper Colorado River: Black Rocks, Westwater Canyon, Cataract Canyon, Desolation/Gray canyons, and Yampa Canyon (USFWS[1]). Over the course of the 20th century, the distributional range of the humpback chub has been reduced by more than 70% as a result of anthropogenic activities in the Colorado River (USFWS[2]). In 1967, the species was listed as endangered by the U.S. Fish and Wildlife Service (U.S. Office of the Federal Register 32:48 [1967]: 4001) and recovery plans were approved in 1990 for the upper Colorado River populations (USFWS[1]). Establishment of additional spawning stocks and eventual recovery of the species depends on a thorough understanding of habitat relationships for all life history intervals of the species. Habitats where humpback chub are found are often swift, deep and turbid; these conditions do not permit direct observation of habitat use and investigators must rely on inference from indirect and relatively inefficient sampling methods, i.e., nets, traps, and electrofishing in riverine environments. As a result, characterization of habitat use by humpback chub has tended to be general, lacking specificity for life history intervals and spawning.

In contrast to sketchy information on the spawning ecology and behavior of the humpback chub and other closely related species of *Gila* (USFWS[1]), there is a wealth of knowledge for many North American cyprinids. Phylogenies of North American cyprinids predict that members of the genus *Gila* are generalized broadcast spawners (Johnston & Page 1993; see Johnston 1999 this issue). There is evidence that *G. cypha* spawns during receding spring and early summer high flows that originate as snowmelt runoff from the western Rocky Mountains (Valdez & Clemmer 1982, Kaeding et al. 1990). Miller et al.[3] suggested that *G. cypha* spawned in the upper Colorado River basin in deep, swift water

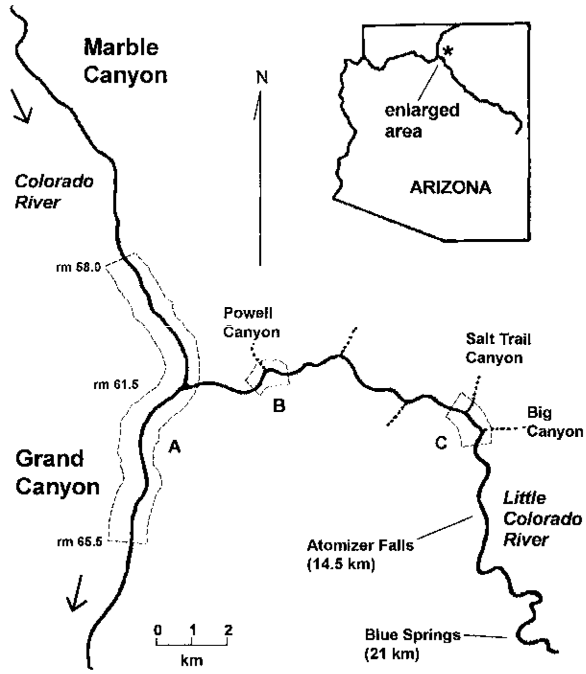

Figure 1. Map of the lower Little Colorado River (LCR) and confluence with Colorado River in the vicinity of Grand and Marble canyons, Coconino County, Arizona. (A) 12 km reach of the Colorado River centered on the confluence of the LCR (CR-LCR confluence), between Colorado River miles (rm) 58.0 and 65.5 and including the lower 200 m of the LCR. Adult humpback chub captured in this reach provided evidence of movement into the LCR during spring months. (B) Lower study reach in the vicinity of Powell Canyon (3 km). (C) Upper study reach in the vicinity of Salt Trail Canyon (10.5 km). Perennial flow (~ 6 m^3 s^{-1}) in the LCR was maintained mostly by Blue Springs. Atomizer Falls marks the upstream terminus of humpback chub distribution in the LCR.

canyons on pockets of clean rubble and gravel. Others have reported evidence of spawning in association with boulder and sand substrates within shoreline eddy habitats (Karp & Tyus 1990); submerged cobble and gravel bars (Valdez & Clemmer 1982, Valdez & Nilson 1982, Kaeding et al. 1990); cobble and gravel along talus shorelines (Valdez[4]); and shorelines composed of large angular boulders (Kaeding et al. 1990). At the Willow Beach National Fish Hatchery, humpback chub spawned in race-

[1] USFWS. 1990. Humpback chub recovery plan. U.S. Fish and Wildlife Service, Denver. 43 pp.

[2] USFWS. 1994. Endangered and threatened wildlife and plants; determination of critical habitat for the Colorado River endangered fishes: razorback sucker, Colorado squawfish, humpback chub, and bonytail chub. 50 CFR Part 17, Final Rule. 21 March Federal Register 59: 13374–13400.

[3] Miller, W.H., J.J. Valentine, D.L. Archer & H.M. Tyus (ed.) 1982. Colorado River fishery project final report summary, Part 1. U.S. Bureau of Reclamation and U.S. Fish and Wildlife Service, Colorado River Fishery Project, Salt Lake City. 42 pp.

[4] Valdez, R.A. 1990. The endangered fish of Cataract Canyon final report. Bureau of Reclamation Contract No. 6-CS-40-03980, BIO/WEST Report No. 134–3, Logan. 172 pp.

ways with gravel and cobble substrates (Hamman 1982).

The largest known population of humpback chub occurs in the lower 14 km of the Little Colorado River (LCR) and the inflow reach of the Colorado River in Grand Canyon (USFWS[1], Douglas & Marsh 1996). Humpback chub reproduce successfully in the LCR, where all life history intervals are found (Kaeding & Zimmerman 1983). In contrast to relatively large flows in the mainstem Colorado River (150–600 $m^3 s^{-1}$), base flow in the LCR is much smaller ($\sim$ 6 $m^3 s^{-1}$), which allows more intensive and quantitative studies to be conducted. The objective of our study in the LCR was to determine spawning ecology and phenology for the species, including habitat use and population movement related to spawning. Such information would be invaluable for establishing additional spawning stocks, particularly by identifying areas within the historic distributional range that contain potential spawning habitat, and by providing guidance for modifying hydrologic conditions in regulated river reaches (e.g., Grand Canyon) to encourage successful spawning.

Methods

Study area

Two reaches were studied in the lower 21 km of the perennially flowing portion of the LCR, located in Coconino County, Arizona, near Grand Canyon (Figure 1). The lower reach was located 2.3–3.4 km above the confluence with the Colorado River near Powell Canyon (36°11′45″N, 111°46′0″W), and the upper reach was 10.5–11.9 km above the confluence near Salt Trail Canyon (36°10′42″N, 111°42′16″W). Mean base flow of 6.31 $m^3 s^{-1}$ is maintained by springs starting at 21 km above the confluence (Cooley 1976). Water from these springs is high in chloride salts, relatively constant in flow and warm (20°C), highly charged with carbon dioxide, and saturated with calcium carbonate (Cole 1975). Travertine deposition in the LCR is an ongoing process, and extensive reefs, terraces, and dams have formed throughout the lower 14.5 km [travertine is massive, layered deposits of hard, dense calcite (Gary et al. 1972)]. Large boulders calved from canyon walls or transported by debris flows from side canyons are common landmarks in the stream channel. Snowmelt in the upper LCR drainage causes flooding in late winter and spring (February-March), when discharge ranges from 15 to >50 $m^3 s^{-1}$. Discharge data from U.S. Geological Survey gage 09402000 near Cameron, Arizona, approximately 70 km upstream from the confluence, were used to calculate weekly mean discharges over 1993–1995. To account for base flow discharge from springs below km 21, 6.31 $m^3 s^{-1}$ was added to weekly mean discharge. Temperature data recorded 1.5 km upstream from the confluence by the U.S. Bureau of Reclamation were used to calculate weekly mean temperatures over 1993–1995.

Sampling design

Spawning phenology and ecology of humpback chub were studied during spring (March-June) of 1993–1995 as part of a larger study in the LCR over 1991–1995. High turbidity prevented direct observation of habitat use by fish, abundant boulder and travertine deposits precluded the use of seines or trammel nets, and high conductivity (>5000 µS cm^{-1}) in combination with deep water (up to 5 m) rendered electrofishing ineffective. However, hoopnets could effectively sample the array of habitats and physical conditions in the LCR. To determine habitat use by adults, we used 'mini-hoopnets' which were 50–60 cm diameter × 100 cm long and made with 3–4 hoops, a single 10-cm throat, and 6 mm nylon mesh. These were arranged in a grid along cross-channel transects established at 20 m intervals (Figure 2). Ropes were stretched across the river at transect locations to aide in deploying nets and conducting habitat measurements (described below). Typically, 25 nets were deployed along 4 transects with staggered set and pull times: half were set in evening and half were set in morning to control for the time of set. Along transects, hoopnets were set as close to stream banks as possible and spaced at 4–5 m intervals across the channel. Each net was emptied twice while in place for

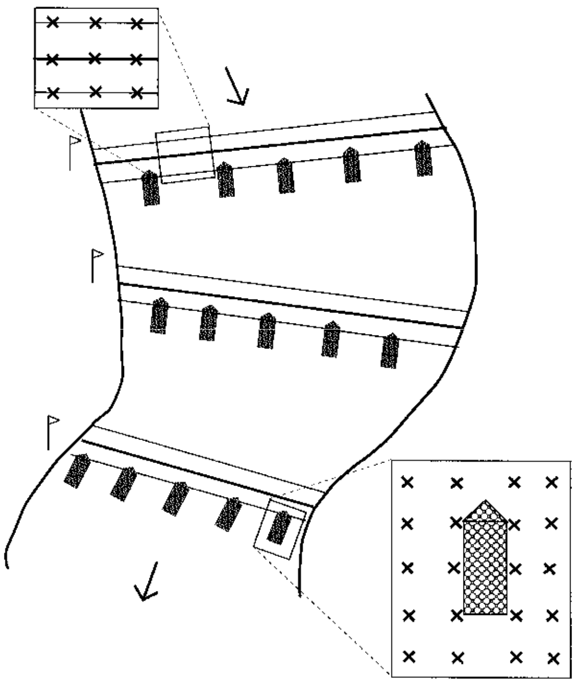

Figure 2. Habitat and fish sampling. Triple lines represent cross-channel transects for sampling available habitat. Cross-channel transects, denoted by flags along left bank, were spaced 20 m apart. Habitat was measured at sample points along the transect at 1 × 1 m intervals (upper left box). Minihoopnets were spaced at 4–5 m intervals along transects. Habitat was sampled around minihoopnets in a 4 × 5 grid of points with 0.5 m spacing (lower right box).

24 h: within 2 h before sunset and within 2 h following sunrise. To sample the entire water column, some nets were anchored on the bottom, others were suspended in the water column, and others were equipped with floats to hold them at the surface. Over 10 day monthly sampling periods, 130–170 net sets were made over about half the length of each study reach (500–700 m) and we sampled alternate sections between months.

Data from both study reaches for the period March-June 1993–1995 were used in analyses of spawning phenology and ecology, whereas only data from the upper study reach for March-May 1993–1995 were used for analyses of habitat use and spatial distribution of adult fish. Seasonal changes in adult stock levels were analyzed using catch data from both study reaches for March-September 1993–1994.

Habitat measurements

Available habitat was sampled at points along each cross-channel transect at 1 m intervals, with additional point samples taken 1 m above and below the transect point to form a 'triple transect' grid (Figure 2). 'Habitat sampled for fish' was assessed by habitat measurements at 20 sample points over a 2.0 x 1.5 m grid around each mini-hoopnet. Habitat use by fish was determined by analyzing habitat data from nets where fish were caught.

Following the methodology of Gorman & Karr (1978), depth, current, and substrate were measured at each sample point. Using a 2 m × 25 mm pole, depth was measured in centimeters, surface current was identified as one of 6 velocity categories, and substrate under the point of the pole was identified as one of 10 size categories. Current velocity categories were defined by patterns of flow around the measuring pole and calibrated with a current meter. Points where the direction of flow was upstream were recorded as eddy currents. Additional substrates present within 10 cm of the measuring pole were recorded for each sample point.

For each mini-hoopnet, the following statistics and frequency counts were derived from the 20 habitat sample points: *Relative depth* (RDPH) is the % of depth from water surface to middle of net throat. One value applies to all points in a net grid. Because the net throat was 25–30 cm above the bottom of the net, no set could be at 100% RDPH. *Mean lateral position* (MLATP) is the mean distance (cm) of the sample points to the nearest stream bank or emergent edge created by an island or large boulder. *Mean depth* (MDPH) (cm), *mean current velocity* (MCURV) (m s^{-1}) and *standard deviation of current velocity* (SDCURV) (m s^{-1}) are self explanatory. *Frequency of eddies* (FEDDY) is the number of points with eddy (reverse) currents. Substrates were presented as frequency variables for four size classes: *fines* (FFINES) (silt to sand; < 0.06 to 2.0 mm), *gravel* (FGRAVL) (> 2 to ≤ 64 mm), *cobble* (FCOBBL) (> 64 to ≤ 256 mm), and *boulder* (FBOULD)(> 256 mm). *Mean travertine* (MTRA) is the mean travertine (TRA) index ; the index ranges from 0 (no travertine) to 5 (boulder-sized travertine). The triple transect and net sampling grids provided information on three-dimensional habitat structure, i.e., *positive vertical angle* (PVA) (degrees) and *standard deviation of depth* (SDDPH) (cm). PVA for a sample point is the maximum positive vertical angle generated by a line along the stream bottom to surrounding points in a grid or to an emergent edge < 100 cm distant. PVA statistics include *mean positive vertical angle* (MPVA) and *standard deviation of positive vertical angle* (SDPVA). SDPVA provides a measure of angular variation of the bottom profile and SDDPH provides a measure of bottom roughness.

Fish measurements

All humpback chub >150 mm TL were tagged with passive integrated transponders ('PIT tags', Biomark, Inc.) as part of a 1991–1995 multi-agency study (Glen Canyon Environmental Studies Phase II) that investigated movement and demographics of humpback chub in Grand Canyon. Fish were weighed (g), measured (mm) for total length (TL), sexed, and scanned for PIT tag identification number. Reproductive condition of each fish was recorded (see reproductive index below). Fish were released within 10 m of capture location. Sex was determined by examination of genitalia which show strong sexual dimorphism in reproductive adult fish (Suttkus & Clemmer 1977). As part of our 1991–1995 LCR study program, we tracked growth of cohorts over 1991–1995 and found that most humpback chub reached sexual maturity after three years at > 200 mm TL; we encountered only five fish < 200 mm TL that had expressible gametes. Because we were interested in habitat use and behavior by sexually mature adult fish, we limited our analysis to fish > 200 mm TL. Our treatment of adult humpback chub is the same as in Kaeding & Zimmerman (1983).

Reproduction

Reproductive condition was determined by scoring reproductive characters for each fish, including relative amount and distribution of tuberculation, intensity and distribution of spawning coloration, distribution of abrasions (ostensibly from spawning activity), determination of gravid condition (enlarged gonads indicated by plump body), determination of ripe condition (freely expressible gametes), and determination of spent condition (reduced gonads indicated by hollow body cavity and no release of gametes). Along with the free release of gametes, fully ripe adults displayed brilliant orange-red spawning coloration over the ventral surface of the body and in the ventral fins, and fine tuberculation was distributed over the head, caudal peduncle and leading edges of the ventral fins. Reproductive classes of adult humpback chub were defined by the range of spawning scores: non-spawning fish (– 4–0) lacked spawning indicators, e.g., no tuberculation, no spawning color, non-release of gametes; near-spawning fish (1–4) were characterized by tuberculation, spawning color, gravidness, and absence of abrasions; ripe fish were classified as ripe-spawning (> 4). Post-spawning fish were identified by spent condition (flaccid, hollow body cavity), abrasion of fins, and absence of tuberculation and spawning coloration and were classified as non-spawning for habitat analyses. We considered free release of gametes (ripe condition) to be an indication of spawning activity (Kaeding et al. 1990). Our sampling protocol allowed us to evaluate diel activity of humpback chub relative to spawning condition.

Relative condition K_n (LeCren 1951) was used to analyze the relationship between relative condition and spawning phenology and spawning score. Relative condition was calculated as a ratio of observed weight over estimated weight, $K_n = W\ (aTL^b)^{-1}$, where W is weight (g) and TL is total length (mm) and a and b are constants. We determined constants a, b with General Linear Regression (SYSTAT[5]) using capture data for adult humpback chub (> 200 mm TL) from both study reaches for the period March-June 1993–1995. For our study, a K_n of 1.00 represents average condition for fish in the spawning period.

[5] SYSTAT. 1996. Systat 6.0 for Windows. SPSS, Inc., Chicago.

Relative abundance and movement

For analyses of relative abundance, catch data were expressed as catch-per-unit-effort (CPUE) and were calculated as (number of fish/number of net sets) × 100. A net set was considered a unit effort since all nets were set and run for 24 h. PIT tag data allowed analysis of recaptures and movement of individuals. PIT tag capture records of adult fish (> 200 mm TL) from both study reaches for the period March-June of 1993–1995 were compared with available (April 1991-May 1996) PIT tag capture records from the Colorado River-LCR confluence area ('CR-LCR confluence'; Figure 1) for evidence of upstream spawning migration. We also examined our PIT tag capture records to assess within- and between-year movement of adults within study reaches. Mean maximum distance between captures within and among years provided a relative measure of movement.

Habitat use

Habitat use by adult humpback chub was evaluated during the spawning season (March-May) of 1993–1995 for the upper study reach only. June data were omitted because there was little evidence of spawning activity (very few ripe-spawning or near-spawning adults were present). The lower study area was not considered in this analysis because of insufficient catches of adults. Frequency distributions of available habitat (measured along transects, Figure 2) and sampled habitat (measured in grids around minihoopnets, Figure 2) were compared with Kolmogorov-Smirnov 2-sample tests (SPSS[6]) (critical p-values set at $p < 0.01$). We found no significant differences that could not be resolved by adjusting available habitat to reflect the inability of our mini-hoopnets to sample areas < 20 cm in depth (areas rarely used by adult humpback chub; Gorman[7]). Thus, we only considered comparisons between sampled habitat (i.e., measured in grids around mini-hoopnets), and used habitat (i.e., data from nets where fish were caught). Differences in distributions of sampled habitat vs. habitat use by reproductive classes of fish (non-spawning, near-spawning, ripe-spawning) were evaluated with Kolmogorov-Smirnov 2-sample tests (SPSS[6]).

Logistic regression analysis (SPSS[6]) was used to assess the effect of habitat variables and reproductive classes on presence/absence of non-spawning, pre-spawning, and ripe-spawning fish. Discriminant function analysis was performed to distinguish non-spawning, pre-spawning, and ripe-spawning fish in multivariate habitat space.

Spatial distribution

Spatial distribution of adult humpback chub captures over the sampling grid during the spawning seasons (March-May) of 1993–1995 provided evidence of intraspecific association (dispersion vs. aggregation) related to spawning condition. Data from the upper study reach were analyzed for patterns of spatial distribution by comparing predicted and observed catches of fish with Chi-square tests with p-values set at < 0.01 (sensu Gorman 1988). First, we determined whether adult fish as a group were spatially dispersed or aggregated. Then, the effect of non-spawning, near-spawning, and ripe-spawning reproductive classes on the spatial distribution of all adult fish were determined. Finally, each reproductive class was evaluated individually to determine whether it was spatially dispersed or aggregated. Landscape-scale distributional patterns of ripe-spawning fish were investigated by locating aggregations of ripe fish (n > 1) and near-spawning fish on a map of the upper study reach showing side canyons and large structural features

[6] SPSS. 1994. SPSS for Windows, release 6.1. SPSS, Inc., Chicago.

[7] Gorman, O.T. 1994. Habitat use by humpback chub, *Gila cypha*, in the Little Colorado River and other tributaries of the Colorado River. Final Report to the U.S. Bureau of Reclamation, Upper Colorado Region, Glen Canyon Environmental Studies, U.S. Fish and Wildlife Service, Flagstaff. 303 pp.

such as travertine dams, travertine reefs, and boulder fields.

Results

LCR fish community

In the two study reaches, humpback chub numerically dominated the LCR fish community: 628 adult (> 200 mm TL), 678 older juvenile (> 100–200 mm TL), and 782 yearling (80–100 mm TL) humpback chub were captured in 1597 net sets over the period March-June 1993–1995. Other native species captured included 1356 speckled dace, *Rhinichthys osculus*, 352 bluehead sucker, *Catostomus discobolus*, and 25 flannelmouth sucker, *C. latipinnis*. Non-native species included 52 fathead minnow, *Pimephales promelas*, and 2 plains killifish, *Fundulus zebrinus*. In nets with adult humpback chub, non-adults and other species were usually present but were fewer and relatively small. The adult humpback chub population fluctuated seasonally (Figure 3); the number of large (> 300 mm TL) and smaller adults peaked in May but the number of large adults dropped to near-zero by August whereas the number of smaller adults only declined by half. Most (463/628) adult humpback chub were captured in the upper study reach and for this reason only data from the upper reach were used for analysis of habitat use and spatial distribution.

Spawning phenology

Seasonal patterns of discharge were similar among the three years, but the magnitude of peak winter and early spring floods in 1993 was approximately 2–5 times that of the other years. Spawning phenology for humpback chub followed changes in discharge and temperature between winter and spring months (Figures 4, 5). Flooding in February and early March, caused by late winter precipitation and snowmelt, declined rapidly during late March-early April. Mean water temperature was < 12°C in February and reached > 20°C by mid-May when base flow was achieved. Proportions of non-, near-

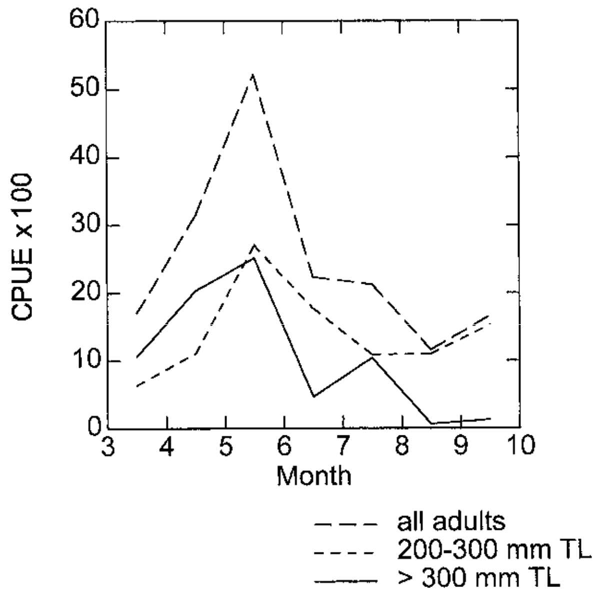

Figure 3. Seasonal changes in abundance and size composition of adult humpback chub in Little Colorado River. Catch per unit effort (CPUE) per 100 net sets are averaged monthly over March-September 1993–1994 for both study reaches. Adults are divided into large (> 300 mm TL) and small (200–300 mm TL) size classes. Total sampling effort was 2225 net sets.

and ripe-spawning fish varied over the spawning season: the proportion of ripe-spawning fish peaked in April at 41%, whereas the proportion of non- and near-spawning fish peaked in May at 84% (Figure 5). In June, when adult stock levels had declined, ripe-spawning fish were almost absent and numbers of near-spawning fish were greatly reduced. Mean relative condition declined rapidly from a high of 1.22 (females)–1.08 (males) in March to a low of 0.99 (females)–0.98 (males) in June. By comparison, mean relative condition for a sample of fish from December was lower (1.06 for females, 1.01 for males) than in March, suggesting that relative condition peaked during winter months prior to spawning. Catch per unit effort (CPUE) of adult fish was low during high discharge in March, increased as discharge declined to base flow in May, but then declined in June to March levels, suggesting movement of adult fish into and out of the study reaches.

In March, low mean spawning scores, the absence of ripe females, high relative condition, and lack of spawning color in females suggested that

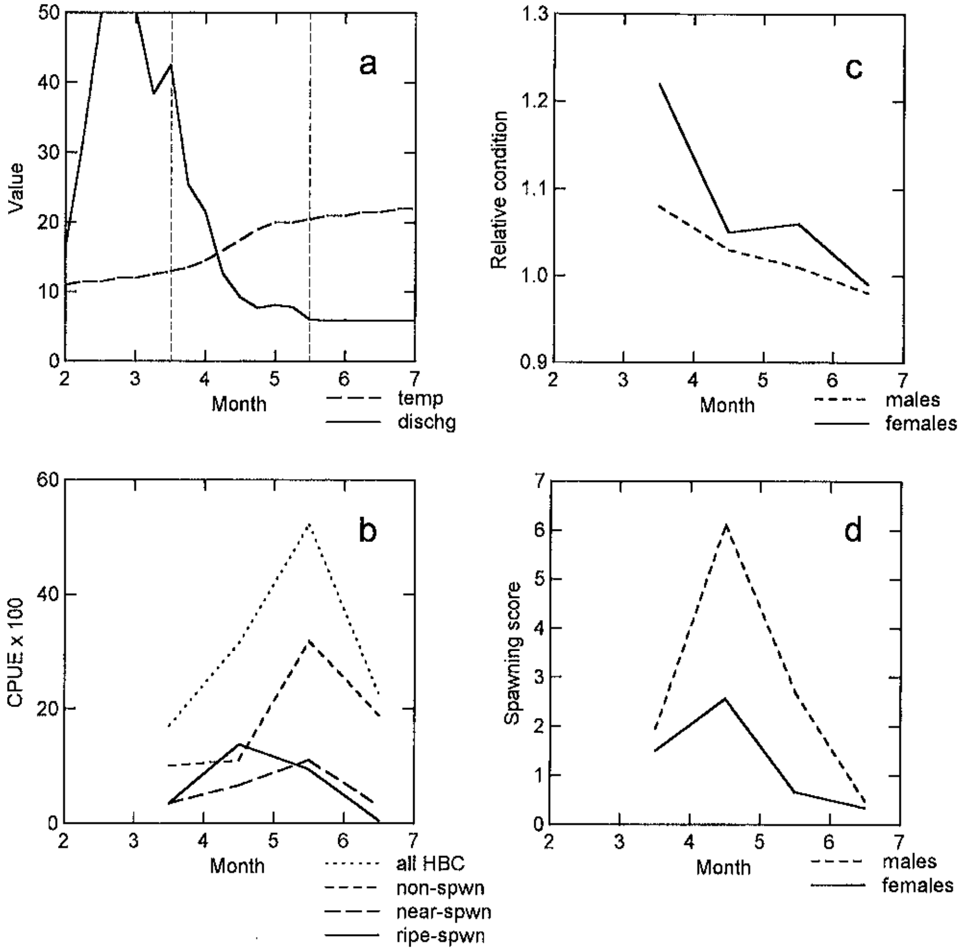

Figure 4. Spawning phenology of adult humpback chub in the Little Colorado River: a - Weekly mean discharge (DISCHG) and weekly mean water temperatures (TEMP in °C) averaged over 1993–1995. Discharge reflects base flow of ~ 6 m^3 s^{-1} from Blue Springs; discharge data from U.S. Geological Survey gauge 70 km upstream. Temperature data from U.S. Bureau of Reclamation station at 1.5 km. Dashed vertical lines indicate interval when ripe fish are present. b – Catch per unit effort (CPUE) per 100 net sets for adult humpback chub (HBC): non-spawning (*non-spwn*), near-spawning (*near-spwn*), and ripe-spawning *(ripe- spwn)* fish. c – Mean relative condition (K_n) adult humpback chub. d – Mean spawning score for adult humpback chub. Criteria for classification of humpback chub in various spawning classes and spawning score are presented in Methods. (b)-(d) use data from both study reaches averaged over the period March-June 1993–1995.

spawning had not yet started (Figures 4, 5). By mid-April when discharge was dropping rapidly and mean water temperature rose above 15°C, there was a sharp decline in mean female relative condition coupled with peaks in mean spawning scores, frequency of reproductive characters, and proportions of ripe fish. The rapid change in the spawning condition of the stock between March and April suggests that spawning must have commenced between late March and early April. Spent females appeared in April, the period of peak spawning activity, and then gradually declined during May and June (Figure 5). Spent males appeared later in May and disappeared in June. In contrast to females, mean spawning scores for males and the proportion of ripe males remained much higher over the spawning season. A decline in reproductive measures to near zero values in June indicated that most adult fish were spent by early summer. This pattern suggests that females rapidly expend their egg supply in March and April whereas males maintain reproductive capability over a longer period.

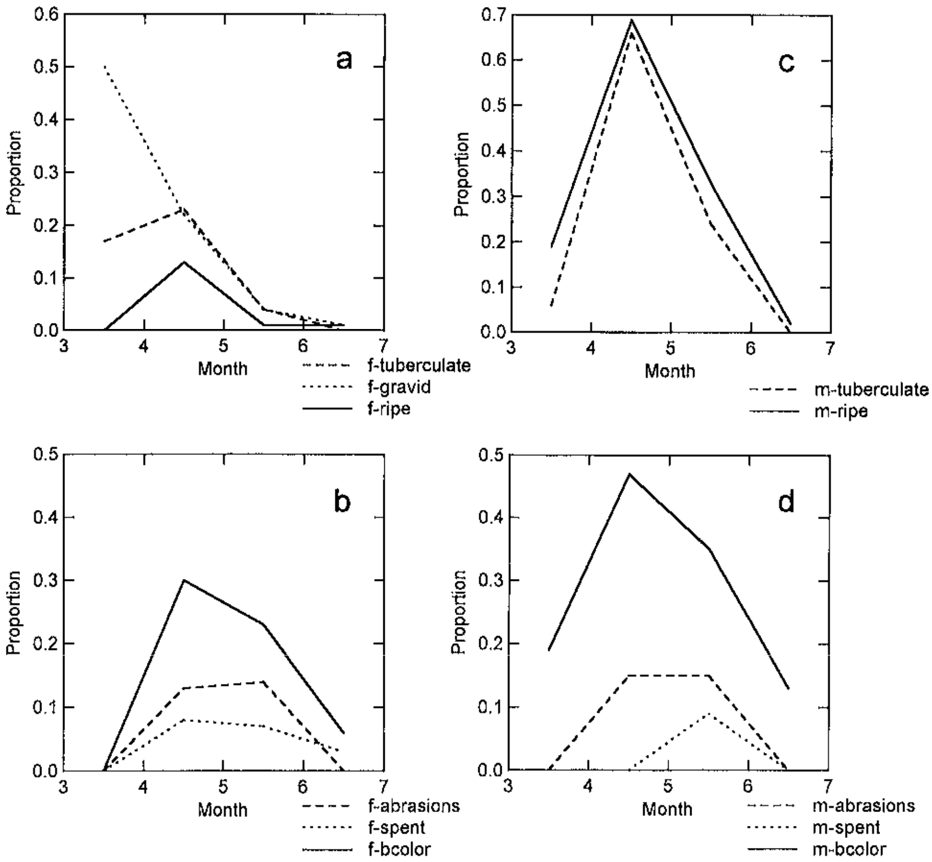

Figure 5. Phenology of spawning characters of adult male and female humpback chub in the Little Colorado River. Spawning characters are expressed as the proportion of male or female stock and are defined in Methods. a, b – Relative frequency of spawning characters for females (*f*). c, d – Relative frequencies for males (*m*) (a– d use data from both study reaches averaged over the period March-June 1993–1995).

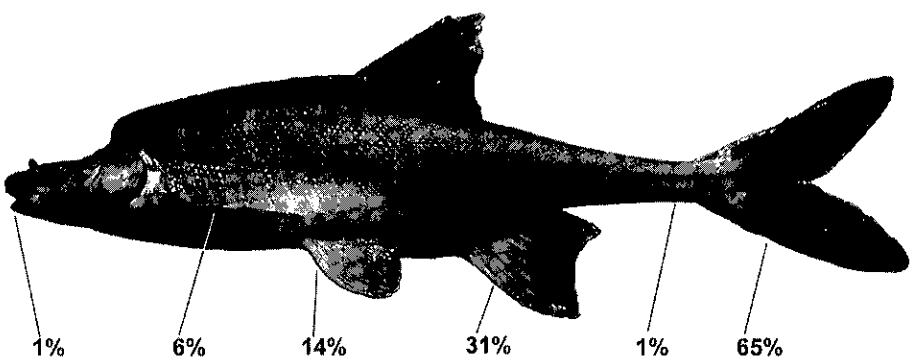

Figure 6. Incidence and distribution of abrasions on adult humpback chub during the spawning season, March-May 1993–1995. Abrasions were found on the leading edges of the pectoral, pelvic, anal, and caudal fins and on the lower lip and caudal peduncle of 72 ripe-spawning, near-spawning, and non-spawning (including spent) adults. Of the 72 fish, 25 (35%) with abrasions were also tuberculate and 34 (47%) were in ripe or gravid spawning condition. Percentages are the proportion of the 72 adults with abrasions at the indicated site. Because many fish had multiple abrasion sites, total % exceeds 100.

Spawning ecology

In both sexes, the incidence of tuberculation mirrored ripeness, although a smaller proportion of females were ripe or tuberculate than males (Figure 5). Incidence of spawning coloration paralleled the rapid increase in incidence of ripe fish but declined more slowly in both sexes. Thus, ripe fish of both sexes were typically tuberculate and in spawning colors. Because a higher proportion of males remained ripe compared to females, more males were tuberculate and in spawning colors than females. The appearance of abrasions during April and May (15% incidence) following the peak in mean spawning scores in April and disappearance of abrasions in June, suggests their association with spawning activity. Almost all observed abrasions were confined to the leading edge of the ventral fins, particularly the caudal and anal fins (Figure 6). The location of these abrasions and the timing of their incidence in the stock suggests that they result from spawning on hard substrate. Nearly 80% of all ripe-spawning fish were captured during night sampling, suggesting that most spawning activity occurs during crepuscular and nocturnal periods (Table 1).

The upper study reach yielded by far the most captures of adult humpback chub during the spawning season (442/568) and thus provided our best example of a spawning stock. There, sex ratios favored females slightly (52:48) (Table 2). Approximately half of all fish were in non-spawning condition and only about one-quarter were in ripe-spawning condition. Most ripe-spawning fish were males (85%) whereas most non-spawning fish (62%) were females. Among males, approximately 46% were ripe and 15% were in near-spawning condition. Among females, only 7% were ripe and 35% were in near-spawning condition. This pattern shows that females in ripe condition were relatively rare compared to males and is consistent with the observation that males maintain ripe condition for longer periods than do females (Figure 5).

Table 1. Differential diel catch rates of adult humpback chub from both study reaches during the spawning seasons (March-May) of 1993–1995. Differences in diel catch rates reflect diel activity patterns. Daytime sampling periods averaged 10 h and night periods averaged 14 h. Number of fish caught per hour (no. h^{-1}) is a relative measure of catch rate for the entire study period. Sampling effort for day and night periods was the same because the same net sampled both periods. Significant differences ($p < 0.01$, Chi-square test, 1 df) in catches for day and night periods adjusted for 10 and 14 h sample periods are indicated with an asterisk.

Spawning class	Day			Night		
	no.	%	no. h^{-1}	no.	%	no. h^{-1}
not spawning	101*	28.0	10.1	260*	72.0	18.6
near-spawning	45	34.1	4.5	87	65.9	6.2
ripe-spawning	25*	16.2	2.5	129*	83.8	9.2
Overall	171*	26.4	17.1	476*	73.6	34.0

Habitat relationships

Habitat use patterns by adult humpback chub during the spawning season were determined from 442 fish captured in 223 of 918 net sets in the upper study reach. Non-, near-, and ripe-spawning reproductive classes used habitat differently from the distribution of sampled (~ available) habitat (Figure 7), indicating strong habitat preferences. Non-spawning fish used areas of slower current, finer substrate (mostly sand) and less structural complexity than was sampled (~ available). Ripe-spawning fish used areas closer to emergent edges as indicated by reduced mean lateral position (MLATP), and used areas containing greater frequency of gravel substrate (FGRAVL) and greater structural complex-

Table 2. Catch summary for adult humpback chub (> 200 mm TL), upper study reach, March-May 1993–1995. A total catch of 442 fish was taken from 223 of 918 net sets (19 fish with unidentified sex are not included below). Percent values to right of each cell represent the percent of the total for that class; percent values below each cell represents the percent of the total for that sex.

Spawning class	male	female	total
non-spawning	78 (38%)	128 (62%)	206
	(39%)	*(58%)*	*(49%)*
near-spawning	30 (28%)	78 (72%)	108
	(15%)	*(35%)*	*(26%)*
ripe-spawning	93 (85%)	16 (15%)	109
	(46%)	*(7%)*	*(26%)*
Total	201 (48%)	222 (52%)	423

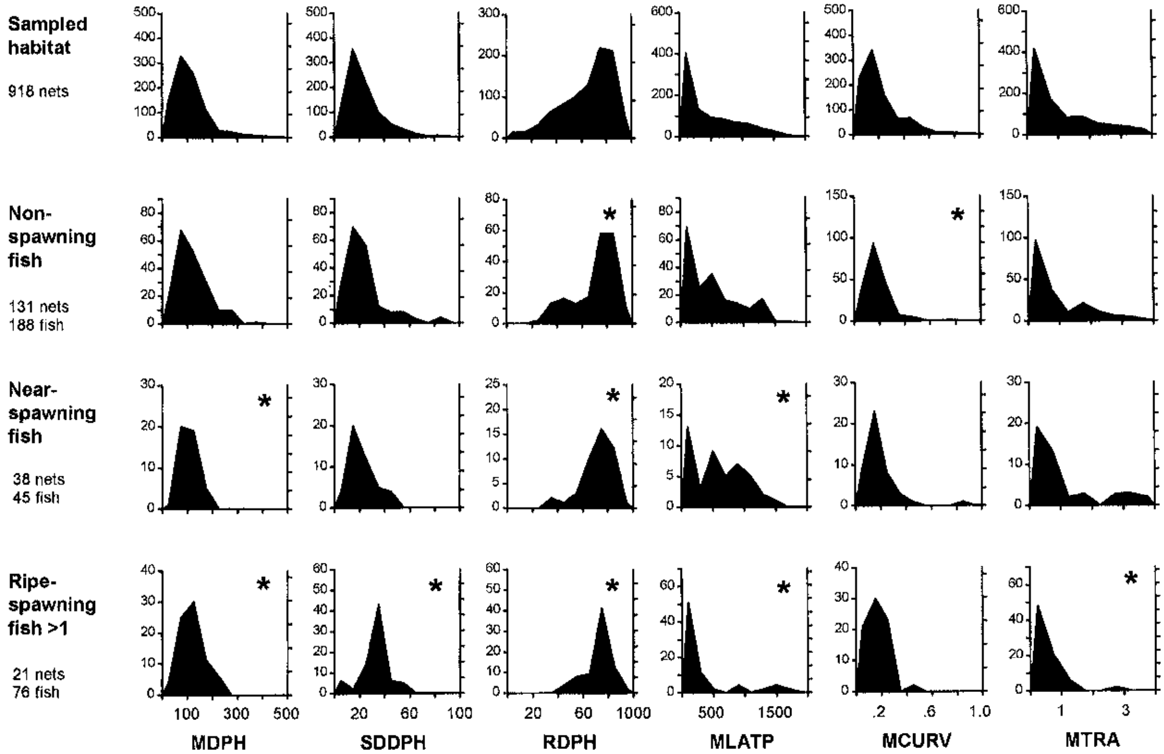

Figure 7. Habitat use by adult humpback chub during the spawning season from the upper study reach, March-May 1993–1995. Asterisks indicate significant differences from sampled habitat distributions, Kolmogorov-Smirnov two-sample test, $p < 0.01$. Habitat variables and reproductive classes are defined in the Methods.

ity as indicated by higher standard deviation of depth (SDDPH), mean positive vertical angle (MPVA), and standard deviation of positive vertical angle (SDPVA) from what was sampled and in comparison to non-spawning fish.

The first set of logistic regression analyses assessed which habitat variables predicted the presence of various classes of adult fish in a net (Table 3a) and were generally concordant with assessment of sampled vs. used habitat distributions (Figure 7). Non-spawning fish were more likely to occur in habitats with a prevalence of fine substrates (FFINES), an absence of eddy currents (FEDDY), and tended to be closer to the bottom (RDPH). Near-spawning fish were associated with increased RDPH and decreased FEDDY. Ripe-spawning fish were more likely to occur in habitats with bottom profiles of increased angular variation (SDPVA), increased frequency of gravel substrate (FGRAVL), and decreased mean travertine (MTRA) and decreased FEDDY. Aggregations of ripe fish ($n > 1$) were associated with increased SDPVA and FGRAVL and decreased FEDDY.

The second set of logistic regression analyses assessed what habitat variables would predict the presence of ripe fish relative to non-ripe fish (Table 3b). Both ripe-spawning fish and aggregations of ripe fish could be distinguished from non-spawning fish by greater likelihood of capture in habitats with increased SDPVA and FGRAVL. Ripe-spawning fish could be distinguished from near-spawning fish by increased mean positive vertical angle (MPVA) and FFINES whereas aggregations of ripe fish could be distinguished by increased SDPVA, FGRAVL and mean depth (MDPH). Habitat selection and segregation analyses showed that predictive variables for the presence of ripe fish were strongly influenced by the inclusion of aggregations of ripe fish in that category. This is evidenced by higher odds ratios for shared predictive variables (SDPVA, FGRAVL) in aggregations of ripe fish and that aggregations could be distinguished from

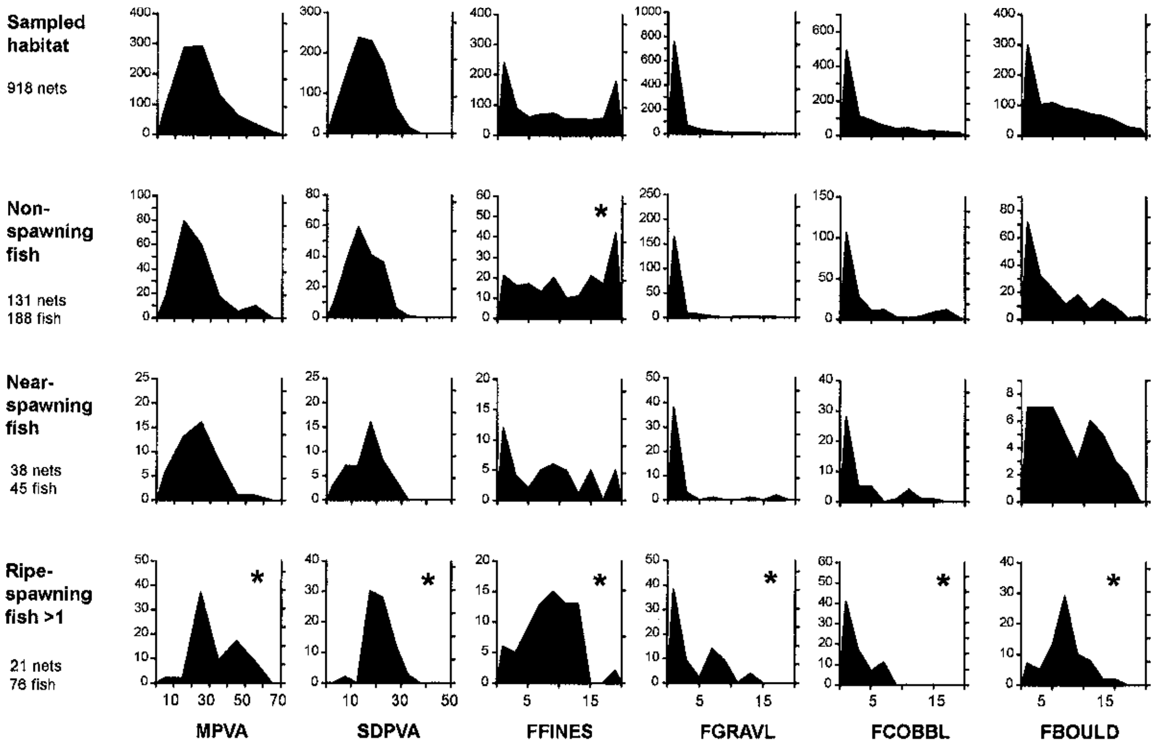

Figure 7. Continued.

near-spawning fish by SDPVA and FGRAVL. Thus, aggregations of ripe fish showed the most distinct pattern of habitat use among the reproductive classes of humpback chub.

The third set of logistic regression analyses assessed the effect of habitat variables and other classes of fish on the presence of ripe fish in a net (Table 3c). Ripe-spawning fish and non-spawning fish were highly spatially segregated, as indicated by a low odds ratio for the effect of non-spawning fish. When non-spawning fish were removed from consideration, near-spawning fish were a significant predictor of the presence of ripe fish in a net. Comparison of aggregations of ripe-spawning fish with nets with one ripe fish also showed near-spawning fish to be a significant predictor of additional ripe fish. Most female fish that occurred in nets with > 1 ripe fish were near-spawning; because of the ambiguity of classifying spawning females, it is possible that many of the near-spawning females in these nets were actually spawning fish.

To corroborate the logistic regression analysis, step-wise discriminant function analysis was used to distinguish non-spawning fish, near-spawning fish, and ripe-spawning aggregations of humpback chub in multivariate habitat space. The most informative habitat variables in separating the groups in the final model, in order of entry, were SDPVA, FGRAVL, MLATP, MTRA, FEDY, MDPH, RDPH, FCOBBL, and MPVA. Canonical Function I explained 83% of the total variance, and like the logistic regression analysis, provided the greatest separation of non-spawning fish and ripe-spawning aggregations based largely on differences in SDPVA and FGRAVL. Interpretation of standardized discriminant function coefficients and location of group means on Function I suggested that aggregations of ripe fish were associated with increased SDPVA and FGRAVL whereas non-spawning fish were not. Canonical Function II explained 17% of the total variance and provided some separation of near-spawning fish from non-spawning fish and aggregations of ripe fish based largely on differences in MDPH, MTRA, FCOBBL, and FEDDY. Interpretation of coefficients and group means suggested that near-spawning fish were distanced from other groups by increased MTRA and FEDDY and decreased FCOBBL and MDPH. Unweighted correct classification of the groups was 74% overall, 85% for non-spawning fish, 22% for near-spawning fish, and 75% for aggregations of ripe fish. The classification results showed that aggregations of ripe fish could be distinguished from non-spawning and near-spawning fish based on differences in habitat use.

Table 3. Variables that predict the presence of adult humpback chub in nets using 'logistic regression' for the Salt Trail Canyon study reach, March-May 1993–1995. Forward step-wise, likelihood ratio variable removal criteria were used to develop logistic regression models (SPSS, 1994). a – Habitat variables that predict the presence of various spawning classes of adult humpback chub of either sex in a net. b – Habitat variables that separate ripe from non-ripe classes of fish. c – Effect of habitat and non-ripe fish on the presence of ripe fish. Of 918 net sets, 695 had no fish, 54 had > 0 ripe fish, 33 had 1 ripe fish, 21 had > 1 ripe fish, 131 had > 0 non-spawning fish in absence of ripe fish, 38 had > 0 near-spawning fish in absence of ripe and non-spawning fish. The odds ratio is the ratio of the probability of finding a fish in a net vs. not. For odds ratios > 1.0, the ratio minus one indicates the increased probability of finding a fish in a net for every unit increase in the variable; for odds ratios < 1.0, one minus the ratio indicates the decreased probability of finding a fish in a net for every unit increase in the variable. Variable codes are explained in Methods.

a. Habitat selection: comparison of nets with fish vs. nets without fish.

Model: dependent / predictor variables	p-value	Odds ratio
non-spawning > 0 vs. fish = 0		
FFINES	0.0091	1.0359
RDPH	0.0062	1.0147
FEDDY	0.0019	0.8955
near-spawning > 0 vs. fish = 0		
RDPH	0.0019	1.0413
FEDDY	0.0470	0.9278
ripe-spawning > 0 vs. fish = 0		
SDPVA	0.0001	1.0888
FGRAVL	0.0000	1.1569
FEDDY	0.0084	0.8556
MTRA	0.0354	0.6887
ripe-spawning > 1 vs. fish = 0		
SDVPA	0.0000	1.1807
FGRAVL	0.0000	1.2396
FEDDY	0.0261	0.6211

b. Habitat segregation: comparison of nets with ripe fish vs. nets with non-ripe fish.

Model: dependent / predictor variables	p-value	Odds ratio
ripe-spawning > 0 vs. non-spawning > 0, ripe-spawning = 0, near-spawning = 0		
SDPVA	0.0005	1.1084
FGRAVL	0.0070	1.1740
MLATP	0.0394	1.0009
ripe-spawning > 1 non-spawning > 0, ripe-spawning = 0, near-spawning = 0		
SDPVA	0.0000	1.1807
FGRAVL	0.0000	1.2396
FEDDY	0.0261	0.6211
ripe-spawning > 0 vs. near-spawning > 0, non-spawning = 0, ripe-spawning = 0		
MPVA	0.0080	1.0584
FFINES	0.0294	1.0928
ripe-spawning > 1 vs. near-spawning > 0, non-spawning = 0, ripe-spawning = 0		
SDPVA	0.0035	1.1914
FGRAVL	0.0120	1.3303
MDPH	0.0073	1.0278

c. Effect of other classes of fish on presence of ripe fish: comparison of nets with ripe fish vs. nets with various spawning classes of fish (non-spawning fish, near-spawning females, ripe females) using habitat and classes of fish as predictor variables. Only those fish variables that were not excluded from either condition in the dichotomous dependent variable could be used.

Model: dependent / predictor variables	p-value	Odds ratio
ripe-spawning > 0 vs. ripe-spawning = 0		
fish variables used: non-spawning fish, near-spawning females		
SDPVA	0.0005	1.0943
non-spawning fish (*n*)	0.0029	0.5173
ripe-spawning > 0 vs. non-spawning > 0, ripe-spawning = 0		
fish variables used: near-spawning females		
SDPVA	0.0014	1.0920
FGRAVL	0.0049	1.1680
near-spawning females (*n*)	0.0279	2.0471
ripe-spawning > 1 vs. ripe-spawning = 1		
fish variables used: non-spawning fish, near-spawning females		
SDDPH	0.0139	1.0679
near-spawning females (*n*)	0.0143	4.1048
ripe-spawning males > 1 vs. ripe-spawning males = 1		
fish variables used: non-spawning fish, near-spawning females, ripe-spawning females		
near-spawning females (*n*)	0.0204	3.5379

Table 4. Summary of adult (> 200 mm TL) humpback chub captures in both study areas and in the CR-LCR confluence, March-June 1993–1995. Recapture records from the CR-LCR confluence are from April 1991-May 1996. The CR-LCR confluence encompasses the lower 200 m of the LCR and 5.6 km above and 6.4 km below the confluence in the Colorado River (Figure 1). The lower and upper study reaches were located 2.3–3.4 and 10.5–11.9 km upstream of the LCR confluence, respectively. Shown are number of individuals captured in CR-LCR confluence/ number of individuals in a reproductive or size class captured in the LCR.

Class	Lower study reach	Upper study reach	Reaches combined
non-spawning	18/87 (20.7%)	35/243 (14.4%)	53/330 (16.1%)
near-, ripe-spawning	15/55 (27.3%)	43/218 (19.7%)	58/273 (21.2%)
≤ 300 mm TL	13/69 (18.8%)	19/227 (8.4%)	32/296 (10.8%)
> 300 mm TL	20/73 (27.4%)	59/234 (25.2%)	79/307 (25.7%)
Total	33/142 (23.2%)	78/461 (16.9%)	111/603 (18.4%)

Movement

Comparisons of our PIT tag capture records (March-June 1993–1995) from both study reaches with records from the CR-LCR confluence for the period April 1991-May 1996 showed that many adult humpback chub migrated upstream during the spawning season (Table 4, Figure 1). Some individuals captured in our study reaches were also captured in the Colorado River 5.1 km upstream and 6.4 km downstream of the LCR confluence. Total migration distance to our upper LCR study reach was ~ 18 km for some of these individuals. Overall, 111 (18%) of 603 adults captured in our study reaches were also captured in the CR-LCR confluence. Greater proportions of near- and ripe-spawning (21%) and large (> 300 mm TL) (26%) adults were also captured in the confluence relative to non-spawning (16%) and smaller adults (11%). A greater proportion of adults in the lower reach was also captured in the CR-CLR confluence compared to the upper reach (23 vs. 17%); this may be a result of closer proximity to the Colorado River (2.3–3.4 vs. 10.5–11.9 km) or because there was a higher proportion of resident adults in the upper study reach.

Examination of our PIT tag capture records also revealed the extent of movement by adult humpback chub within and between our study reaches. Overall, 16 % (97/603) of all individuals were recaptured in the study reaches. Mean maximum recapture distance within reaches was 172 m (n = 68) within years and 325 m (n = 44) between years. Some adults (n = 7) recaptured between years were also captured in the LCR confluence; their mean recapture distance within the study areas was 356 m. Only 2 of 97 individuals that were recaptured were captured in both study reaches, demonstrating a lack of movement between reaches. These results suggest that during the spawning season, adult humpback chub remain within a relatively short section of the LCR and show fidelity to these areas between years.

Spatial distribution

During the spawning season, the spatial distribution of adult humpback chub in the upper study

Table 5. Spatial distribution and intraspecific association of adult humpback chub, upper study reach, March-May 1993–1995. Using the overall catch rate of 1.98 fish net^{-1} as the expected, relative clumping or dispersion was evaluated over the 223 nets that captured fish. Distribution of fish was evaluated within and across spawning classes. For non-spawning and near-spawning classes, nets containing ripe-spawning fish were excluded from the analysis. Significant differences from the overall catch rate ($p < 0.01$, Chi-square test, 1 df) is indicated with an asterisk. Evaluation of the distribution pattern is shown under *dist* column: e = not different from expected (1.99 fish net^{-1}); d = significantly dispersed; c = significantly clumped.

Reproductive class	no. nets	Within class			Across classes		
		no. fish	no. net^{-1}	dist	no. fish	no. net^{-1}	dist
all fish	223	–	–	–	442	1.98	–
non-spawning	131	188*	1.44	d	223	1.70	e
near-spawning	69	80*	1.16	d	126	1.82	e
ripe-spawning	54	109	2.02	c	174*	3.22	c

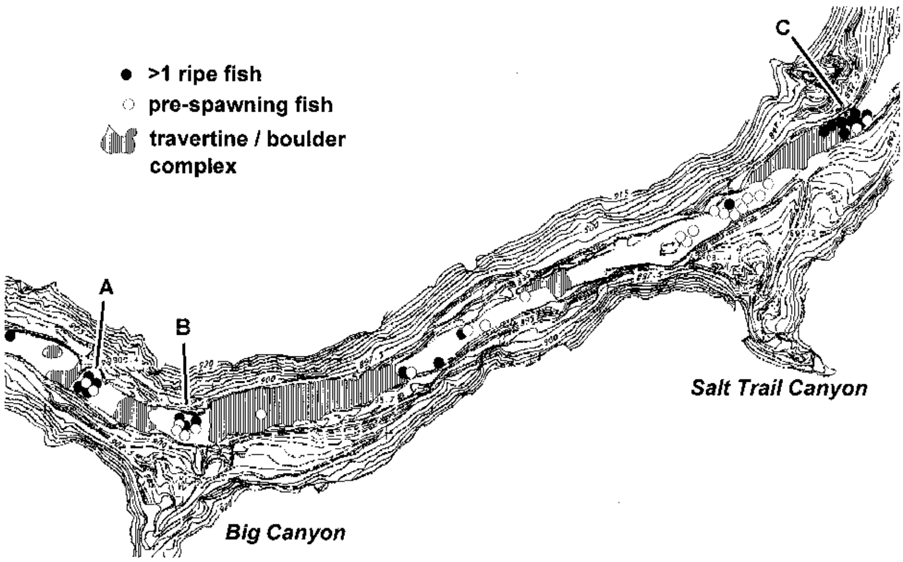

Figure 8. Distribution of spawning aggregations and individual capture locations of near-spawning humpback chub during the spawning season in the upper study reach, March-May 1993–1995. Spawning aggregations were defined as locations where > 1 ripe-spawning fish were captured together in the same net. Clusters of spawning aggregations were found in each of the three years' sampling at sites A (*Hell Hole*), B (*Big Canyon*), and C (*Salt Trail Canyon*). At each cluster site, there were at least two instances of ripe males and ripe females captured together in the same nets.

reach was significantly clumped; on average, 1.98 fish net^{-1} were caught in nets that had fish (Table 5). The presence of non-spawning and near-spawning fish had no effect on clumping, but the presence of ripe fish increased clumping significantly (3.22 fish net^{-1}) and was greatest when a ripe female was present (3.92 fish net^{-1}). An evaluation of captures within spawning classes showed that non-spawning and near-spawning fish were significantly dispersed relative to the population overall (1.44 and 1.18 fish net^{-1}, respectively) while ripe-spawning fish were not.

A closer examination of the distribution of ripe-spawning fish captured during the spawning season showed that 70% (76/109) were aggregated, i.e., captured in multiples in the same nets and most of these, 86%, were males. Overall, 76 ripe fish were captured in multiples in 21 net sets (3.62 ripe fish net^{-1}). For ripe males and ripe females captured together, 18 males and 9 females were captured in 6 nets (4.50 ripe fish net^{-1}). Nets with > 1 ripe fish yielded the highest catch rates for all classes of adult fish (5.43 fish net^{-1}). Non-spawning and near-spawning fish comprised 33% of the total catch in nets with > 1 ripe fish but most of these non-ripe fish (25/38) were females. These results suggest that ripe males are highly clumped and aggregations of males are attractive to both ripe and non-spawning fish.

Distribution of adult humpback chub during the spawning season relative to landscape features in the upper study reach was investigated by locating aggregations of ripe-spawning fish (n > 1) and near-spawning fish (n > 0) on a map of the stream channel showing travertine complexes and boulder fields (Figure 8). Of 21 sites with aggregations of ripe-spawning fish, 17 were located near (< 40 m) or within major travertine-boulder complexes. The locations of aggregation sites in relation to travertine-boulder complexes were consistent among years such that they occurred in each of the three years of study and formed three major clusters (A-C, Figure 8). Cluster A is below a travertine dam. Clusters B and C are at the mouths of Big and Salt Trail canyons; occasional debris flows from these canyons transporting large boulders into the LCR channel upon which travertine deposits create structurally complex habitats. Transects containing the three clusters comprised only 68 m or 5% of the upper study reach but nets set along these transects captured 68% of the ripe-spawning fish, 42% of adults > 300mm TL, and 36% of fish also captured in the CR-LCR confluence. Thus, for each cluster detected per year, there were on average 2 aggregations, 11 large adults, 8 ripe fish, and 3 fish that migrated from the Colorado River. All observed cases of ripe females caught together with ripe males occurred within the three clusters (2 in each). Because freely expressible ova provide good evidence of spawning activity (Kaeding et al. 1990), the locations of these clusters represent prime spawning areas for humpback chub in the upper study reach.

Discussion

Our study has provided a spawning phenology for humpback chub in the LCR (Table 6). During late winter-early spring when discharge is elevated and mean water temperatures are below the 15°C required for spawning and incubation of eggs (Hamman 1982, Marsh 1985), humpback chub achieve their highest relative condition. Spawning apparently commences during mid-March to mid-April, when mean water temperatures rise above 14°C and often while discharge remains elevated. Spawning activity in the LCR peaks as discharge approaches base flow in April, as evidenced by peak densities of ripe-spawning fish and peak mean spawning scores. Increased incidence of abrasions along leading edges of ventral fins in April and May provides evidence of April spawning activity. Spawning activity wanes in May, as indicated by declining mean relative condition and mean spawning scores and an increased density of non-spawning fish. Estimated dates of spawning based on examination of humpback chub larvae support our proposed timing of spawning activity (Robinson et al.[8]). The temporal pattern of humpback chub spawning relative to discharge and temperature in the LCR is similar to that observed for humpback chub in the upper Colorado River basin, except that declines in peak discharge and increased water temperatures there do not occur until May-July, at which time spawning occurs (Kaeding et al. 1990, Karp & Tyus 1990).

The increase in catch rates of adult humpback chub from March through May and the sharp decline in June suggests that adult fish, particularly large (> 300 mm TL) adults, move into our study reaches to spawn and then depart. While post-spawning catches of large adults declined to near-zero by August, catches of smaller (> 200–300 mm TL) adults declined only by half, suggesting that

[8] Robinson, A.T., R.W. Clarkson & R. E. Forrest. 1996. Spatiotemporal distribution, habitat use, and drift of early life stage native fishes in the Little Colorado River, Grand Canyon, Arizona, 1991–1994. Final Report to the U.S. Bureau of Reclamation, Upper Colorado Region, Glen Canyon Environmental Studies, Flagstaff, Arizona, Cooperative Agreement No. 9-FC-40-07940, Arizona Game and Fish Department, Phoenix. 69 pp.

Table 6. Summary of spawning phenology and ecology of humpback chub in the LCR. Maximum value is indicated by ● and reduced value is indicated by ○. No symbol indicates absence. *Pre-spawn* fish are typically gravid with some breeding coloration and tuberculation. *Spawning* fish are typically ripe, in breeding coloration, and fully tuberculate. *Post-spawn* fish are typically spent, lack tuberculation, have reduced level of color, and have abraded fins. *CR* - Colorado River- LCR confluence reach (Figure 1).

	Winter	March	April	May	June	Summer	Fall
Temp. °C	11	13	15	20	22	22	15
Discharge	●	●	○	○	○	○	○
Gravel	●	●	●	○			
Pre-spawn ♂	●	●	○				
Pre-spawn ♀	●	●	○				
Spawning ♂	○	●	●	●	○		
Spawning ♀		○	●	○			
Post-spawn ♂				○	●		
Post-spawn ♀			○	●	●		
Adults – LCR	○	●	●	●	○	○	○
Adults – CR	●	○	○	○	○	○	●

many smaller adults remain resident in the LCR. Comparisons of our PIT tag capture records with those from the CR-LCR confluence provided evidence of migration of adults (especially > 300 mm TL) to our study reaches ~ 3–13 km upstream in the LCR during the spring spawning season. Valdez & Ryel[9] and Douglas & Marsh (1996) provided evidence that humpback chub congregate in the LCR confluence during March-April. Valdez & Ryel[9] showed that some of these fish ascend the LCR as far as 13 km and then return to the Colorado River sometime after the spawning season. As with our study, Douglas & Marsh (1996) found evidence of upstream movement of humpback chub in the LCR during spring and a high level of stasis of individuals within their sample reaches. They also found that a portion of the population remains resident throughout the year; however, we found that the resident portion was composed almost entirely of smaller adults. Our findings that show limited movement of adults within study reaches, fidelity to stream sections between years, and aggregations of ripe adults at the same sites among years must be reconciled with evidence of annual spawning migrations by a large proportion of the adult humpback chub population from the Colorado River into LCR. The higher proportion of large adults relative to smaller adults (26% vs. 11%) that were also caught in the CR-LCR confluence suggests age/size specific differences in life history traits, i.e., younger, smaller adults remain resident in the LCR and as they approach 300 mm TL, they shift fall and winter residency to the Colorado River mainstem and migrate into the LCR during the spring, return to specific upstream locations to spawn, and then return to the Colorado River by late summer. Analyses of length-frequency distributions and size-specific survivorship in the maintem humpback chub population by Valdez & Ryel[9] support this shift in residency as adults approach 300 mm TL. Movement and fidelity to specific locations during the spawning season between years has also been observed by Karp & Tyus (1990) for humpback chub in the upper Colorado River basin.

The most primitive and common spawning mode in cyprinids is broadcasting (Johnston & Page 1993; see Johnston 1999 this issue). Observations of broadcast spawning in the endangered bonytail chub, *Gila elegans*, may provide insight for spawning behavior in the closely related humpback chub. In May of 1954, Jonez & Sumner[10] observed up to 500 bonytail chub spawning at depths up to 9 m over an extensive gravel shelf in the then relatively new Lake Mohave reservoir on the lower Colorado River. They noted that within this mass aggregation, smaller aggregations of 3–5 males escorted a single female and spawned and broadcast semi-adhesive eggs over gravel substrate. Like many other cyprinids, ripe humpback chub males in the LCR appeared to form spawning aggregations in areas with clean gravel deposits, but unlike bonytail chub, we found no evidence of mass aggregations. In the LCR, relatively small aggregations (~ 2–6 fish) or clusters of aggregations of ripe-spawning fish occurred in the spring (March-May), were numerically dominated by males, and the locations of most aggregations were consistent among years. We assumed that aggregations that included ripe males and ripe females provided the strongest evidence of spawning activity. Aggregations were located in areas of moderate depth (1–2 m) where travertine reefs and numerous boulders contributed to high structural complexity and angular variation in the bottom profile. Most near-spawning (including gravid) females used different habitats than did aggregations of ripe fish and were similar to non-spawning fish in that their habitats were more mid-channel and away from emergent edges and had less structural complexity. Also, near-spawning (including gravid) females tended to be found in areas with more travertine deposits that lacked gravel substrate. Despite strong differences in habitat use

[9] Valdez, R.A. & R.J. Ryel. 1995. Life history and ecology of the humpback chub, *Gila cypha*, in the Colorado River, Grand Canyon, Arizona. Final Report to the U.S. Bureau of Reclamation, Salt Lake City, Utah. Contract No. 0-CS-40-09110. BIO/WEST Report No. TR-250-08, BIO/WEST, Inc., Logan. 286 pp.

[10] Jonez, A. & R.C. Sumner. 1954. Lakes Mead and Mohave investigations: a comparative study of an established reservoir as related to a newly created impoundment. Federal Aid Project Report F-1-R, Nevada Fish and Game Commission, Reno. 187 pp.

among reproductive classes, mapping capture locations revealed that they were often in close proximity (< 50 m) to one another, especially near-spawning fish and aggregations of ripe fish. Our results are concordant with previous observations in the upper Colorado River basin of the association of humpback chub in reproductive condition with rapidly flowing water among large angular boulders and shoreline outcrops (Kaeding et al. 1990), or along shoreline eddy habitats that averaged 1.3 m depth with swirling currents and sand and boulder substrates (Karp & Tyus 1990).

The patterns of distribution by sex, reproductive condition, and habitat observed in this study suggest the following scenario for the spawning ecology and inferred behavior of humpback chub in the LCR: Spawning habitat typically occurs below large travertine dams and reefs in association with gravel substrate. These areas are strewn with large angular boulders and travertine structures that form a complex channel configuration with a matrix of plunge pool, chute, run, and eddy habitats and depths ranging from 0.5–2.0 m. During winter and early spring floods, strong hydraulics cause windrows of clean gravel to deposit behind or around large boulders and travertine structures. As the river begins to return to near base-flow conditions in March-April, tuberculate ripe males in spawning coloration aggregate at sites containing gravel substrates. When gravid females ovulate, they move to these aggregations, perhaps guided by the scent of milt from ripe males (see Rakes et al. 1999 this issue). These ripe females, usually tuberculate and in spawning coloration, may spawn with 2 or more males simultaneously. Spawning most likely occurs during crepuscular or nocturnal periods, and based on patterns of fin abrasion, both sexes probably contact gravel or other substrate during the spawning act to deposit and fertilize semi-adhesive eggs. It is unlikely that males guard these sites. Once the immediate supply of ripe eggs is expended, females retreat to nearby habitats where they join other near-spawning and mostly female non-reproductive fish. This cycle of spawning behavior is repeated by individual fish until the supply of eggs and sperm is exhausted, usually by mid-May.

Our study has identified spawning migration and putative spawning habitat and provided a preliminary description of spawning ecology and behavior for humpback chub in the LCR. Future field studies need to apply these findings and more precisely locate spawning sites in the LCR, e.g., sample gravel substrates in areas of spawning aggregations for presence of eggs and developing embryos, conduct visual observations of spawning behavior, and refine the spawning pattern we have identified. Further analysis of all available PIT tag capture records from the CR-LCR confluence will provide a more detailed picture of spawning migrations and the relative contribution of Colorado River fish to reproduction of humpback chub in the LCR. Application of GIS techniques in conjunction with habitat surveys in the LCR will allow quantification of available spawning habitat in that system. Our results should be applied to other areas of the Colorado River where humpback chub populations persist to better understand the ecology of the species and thereby further recovery efforts.

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